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THE MODIFICATION OF VEGETATIVE AND REPRODUCTIVE FUNCTIONS UNDER SOME VARYING CONDITIONS OF METABOLISM[1]

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In virtually any text on the subject of plant physiology may be found paragraphs dealing more or less definitely or indefinitely with the functions of the so-called essential elements. Many of these treat of the relationships which specific elements or compounds have to the modification of reproductive or of vegetative functions, considering these either as separate entities or as mutually interdependent. Large numbers of contributions dealing with specific phases of the subject are constantly forthcoming from the fields both of research and of practice. Some of these are in the nature of deductions made largely on hypothetical grounds while others are based upon experiments of varied nature. The field which can be well covered by any investigator is limited, though the opportunity for constructive work is large. Much must be done in the way of assembling and interpreting the results of various investigations, especially in connection with the extended researches in chemistry, physics, and the related sciences on the one hand and with the practices of the applied sciences on the other.

Granting all this, it is self-evident that at this time we can scarcely do more than state the problem as it now seems to exist, and take a brief look at its possible future development. As time goes on it seems less and less possible to express any dogmatic opinions, or to draw any narrowly circumscribed conclusions from the data available.

Disregarding the notion that any circumstance which threatens the life of a plant causes such a plant to become markedly reproductive in order that the species may be perpetuated, one of the earliest attempts to explain, on a physiological basis, the apparently interrelated phenomena of vegetative extension and the differentiation of parts more intimately concerned in sexual reproduction, assumed that any of the higher green plants is in a state of adjustment between the materials which it derives from the soil and those substances which it manufactures from these ma-

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terials combined with elements from the air. These two classes of materials were sometimes spoken of as unelaborated and elaborated foods respectively. In general it was stated that if the unelaborated foods predominated, then the plant would tend toward the vegetative condition, whereas if the reverse were true, reproductive structures would be produced. Somewhat later this conception became more concise; nitrogen was considered as being the element among the unelaborated materials which was most effective in producing the vegetative condition, and the several types of carbohydrates were designated as the significant elaborated foods. Thus, in spite of the fact that certain experiments showed the fallacy of the notion, it was assumed that whenever leafy, succulent structures were desired, fertilizers containing nitrogen would produce the result, but that such fertilizers were to be withheld and others rich in potash and phosphorus supplied when fruit production was sought. The whole conception carried with it the idea that the two functions of vegetative extension and sexual reproduction were in some way antagonistic, and statements to that general effect may be found widely scattered throughout the literature of both botany and horticulture. Such an idea may have arisen from the general observation that when the expression of one or the other of these functions is reduced the other is apparently increased relative to an assumed average. Actually such a condition is generally unreal, for while it may be true that certain individual plants in a vigorously vegetative condition may produce fewer sexually-reproductive parts, it by no means follows that suppression of vegetation in itself will mean increased production of reproductive portions or fruitfulness. In fact it is quite possible to suppress reproduction and vegetation in direct relation one with another. In other words, it is not the mere decrease of vegetativeness that induces the production of parts concerned in sexual reproduction, nor the increase of sexual reproduction which decreases vegetative extension, but there is an underlying cause upon which each rests; both may be readily increased or decreased simultaneously, or one can be made to dominate the other through any one or more of several different means.

The recognition of this fact became general when clear-cut quantitative results of definite experiments showed that under certain circumstances the yields of fruit from the higher plants could be greatly increased when nitrogenous fertilizers were applied to them. More critical investigation and chemical analyses indicated that those plants which would respond in this manner were weakly vegetative and that their nitrogen content relative to their dry weight (or, as also shown, to their content of sugars and starch-like complexes) was very low. When the nitrogenous fertilizers were applied, however, the total relative nitrogen content of the plants increased, the plants becoming more strongly vegetative and more fruitful. These findings resulted in a third conception concerning the relationship of nitrogenous and carbohydrate compounds to vegetation and fruiting,

namely, that if plants possess or are capable of synthesizing large carbohydrate reserves but available nitrogen is limited, then, when such nitrogen is supplied, vegetativeness and fruitfulness are both increased. It should be noted, however, that though the nitrogen content may be too low for fruiting, there is frequently an active and abundant differentiation of parts more particularly concerned in sexual reproduction such as buds, flowers, spores, and the like, in these carbohydrate-high plants, and that often such plants are not only more easily multiplied by vegetative means but actually tend more freely to produce specially modified, vegetatively reproductive structures.

On the basis of theory, it should be possible to conceive of at least one more relationship which might exist between the carbohydrate and nitrogenous materials, namely an abundant source of the latter but a meager supply or even a lack of the former. Such a condition actually does prevail at least for the non-saprophytic or non-parasitic higher plants when there is not sufficient light for synthesis of carbohydrates, or when these are limited or removed through insect attacks, pruning, or other agencies. The plants are weakly vegetative and non-reproductive. In the case last previously discussed, nitrogen and not carbohydrates constituted the limiting factor to growth and reproduction, and both were capable of being increased through the application of nitrogenous fertilizers; but in the instance now under consideration neither vegetativeness nor sexual reproductivity is increased by additions of nitrogen; it is only when conditions are provided such that carbohydrates may be formed in greater amount, or are directly supplied, or at least are not artificially removed, that the plants become first vigorously vegetative, and with opportunity for further increase and accumulation of the carbohydrates in relation to the nitrogenous nutrients they become sexually reproductive. Because of the failure clearly to differentiate between these two types of the weakly-vegetative non-reproductive condition, much of the conflict of ideas regarding the means by which vegetativeness or reproductiveness may be regulated seems to have arisen, but on the present conception it is an easy task to harmonize the results from many experiments which seemingly are at variance, or to explain why apparently the same practice may yield widely varying results

Categorically summarizing the foregoing considerations, on hypothetical grounds supported by a limited number of definite chemical analyses made on tomato and on some other species of plants, and on the basis of various suggestions by many workers, we have the following:

Class I. Though there be present an abundance of nitrogenous nutrients, with a low carbohydrate supply, vegetative extension occurs but slowly and sexual reproduction scarcely at all. There is complete or nearly complete absence of blossoms, vegetation is weak, the stems are very slender in comparison to their length and are soft and succulent with little

woody tissue, the leaves are slender and light gray-green. Such plants are practically without the more complex reserve carbohydrates, and are high in moisture, in total nitrogen, and in nitrate nitrogen.

Class II. When there is present an abundance of nitrogenous nutrients and available carbohydrates, both are utilized in vigorous vegetative extension with little or no tendency toward sexual reproduction. The plants produce no sexual parts or a few frequently abnormal flowers or flower clusters which very often are partially transformed into leaves or stems, and very rarely set or mature fruit; they are exceedingly vigorous vegetatively, have stems of large diameter, soft and succulent with a small amount of woody tissue, and large, soft, and intensely dark green leaves. Such plants are relatively low in reserve carbohydrates but are higher than those of Class I, are high in moisture, in total nitrogen, and in nitrate nitrogen.

Class III. When there is a limitation of the nitrogenous nutrients in relation to the available carbohydrates, so that the latter can accumulate in excess of their utilization in vegetative extension, then the plants become sexually reproductive as well as vegetatively active. The plants produce many good-sized blossoms, a large proportion of which set and mature; are less vigorously vegetative than those of Class II; the stems are of large diameter but firm to the touch and with considerable woody tissue; the leaves are large, and dark to light green in color. Such plants contain greater quantities of reserve carbohydrates than those of Class II, but are lower in moisture, in total nitrogen, and in nitrate nitrogen.

Class IV. When there is a further relative reduction of the nitrogenous nutrients without inhibiting a possible increase of carbohydrates, there results a large accumulation of the latter, a decrease in vegetative activity and in sexual reproduction. Such plants produce few small-sized blossoms, a large proportion of which either fail to set and mature, or mature into small, tough fruits; they are feebly vegetative, the stems are of small diameter, very firm and hard to the touch with relatively much woody tissue; the leaves are small, stiff, and light green or yellowish in color. Such plants contain large quantities of the more complex carbohydrates, but are low in moisture and in total nitrogen and are almost completely lacking in nitrate nitrogen.

Naturally these classes, depending as they do upon a quantitative relationship of various substances within the plant, blend insensibly into one another according as these relationships are varied, but what might be called the mid-points within them are very distinct. What departures from these groups may occur when either light or temperature is made a limiting factor can not be stated, but they can be duplicated in soil, sand, or water culture. The term nitrogenous nutrients is used because at the present time it is not definitely known what forms the effective nitrogen may have within various plants. In some, great vegetative extension is associated with nitrogen in the nitrate form. Of course it is not assumed

that carbohydrates and nitrogenous nutrients are the only compounds concerned in the varying expression of vegetative and reproductive functions. The results of recent experiments on the application of sulphur to certain leguminous crops, as well as those from the use of potash, phosphorus, and many other substances, would refute any such idea; they were considered in detail simply because there are available a large number of ponderable analyses concerning them and because they have long been favorite material for speculation.

To determine the rôle of water in respect to the varied plant functions is in itself a large problem. Not only must its direct effects in so far as it enters into chemical combination be deciphered, but a knowledge of its physical influences and of its direct consequences in the rendering available or non-available of other materials is also imperative. The effects of light and temperature, both on vegetation and on reproduction, will undoubtedly eventually find their clearest interpretation when studies have been made relative to the influence of these agencies on internal composition, and to how they are related to observed changes. How either light or temperature reacts upon the type and rate of water and salt absorption, upon the relative proportions of salts absorbed, and upon the processes of photosynthesis, metabolism, and storage, remains in large part still to be exactly determined. Then, too, what limits to the range of expression of any character, or function, or groups of characters or functions, are imposed by hereditary factors on the one hand, or by physiological factors on the other—if actually there is a possibility of separating them—remains for the geneticists, cytologists, and physiologists to determine.

From the physiological and morphological viewpoint, the several contributions by Klebs at once come to mind as being the most outstanding, both because of the range of forms investigated and of the number of environmental conditions considered. It is to be regretted that his work has not contributed a larger mass of data concerning the actual internal conditions and composition of the plants investigated. For the most part he has examined external conditions and external responses, and from the data thus obtained reasoned as to what might be the most probable internal situations and effective elements in producing the observed results.

Several other workers, however, have published analyses of plant tissues, such as the apple, the olive, and other species, on the basis of which it is possible definitely to correlate in a quantitative way the vegetative or reproductive tendencies of such forms with certain elements of their composition. There are also scores of recorded analyses of various plants which show the wide variations in composition of any particular species or variety at various stages of its development or maturity. It is unfortunate that many of these results are fragmentary and do not form a part of a series sufficiently long to admit of determining the range of effects of specific substances under a varied set of conditions. Nor are they sufficiently

detailed, in many cases, to afford real clues as to the several forms in which an element may be present; a total nitrogen estimation alone, for example, is of very little significance in any attempt to determine the nitrogen metabolism of a plant. And yet, invaluable aid toward an interpretation of the problem under discussion can be gained by fitting together the records available, and many of the more recent contributions are very helpful. Specific quantitative measurements of substances frequently take on an entirely new significance when they are no longer considered by themselves alone, but rather in connection with other materials present, as ratios. When, for example, such suggestive results as have come from various experiments designed to determine the nutrient salt requirements of plants in various stages of development, under varied conditions of light and temperature and moisture, are finally coupled with analyses of the organic and inorganic materials in the plants themselves at these different stages of development, we shall have begun a genuine approach to the problem of metabolism.

At the outset of any experiment which concerns the functions of growth or of reproduction, it is quite as important to determine the condition, or better the composition, of the plants which are to serve as the basis for the investigation, as it is to know and control the external conditions imposed. Many of the apparently discordant results of various experiments are easily accounted for and harmonized when the composition of the material used as the basis for investigation is taken into account, or when the range of effects of any element is considered in connection with the limits imposed by other substances present. One has but to think of the effects of nitrogen as partially detailed previously, or of sulphur, or phosphorus, or other elements which enter into a vast number of organic compounds essential to growth, and of how they influence subsequent development when present in varying relative quantities.

At this time it is worth while to consider several points in connection with the analyses of tissues of plants and what these may show. The fact that plants require or absorb mineral salts in varying ratios, quantities, or proportions, means, in other words, that such absorption and utilization depend in considerable measure upon the composition of the plant itself, and will vary as such composition is varied. Changed or changing condition or expression is the external evidence of changed or changing composition. The living plant is constantly in a state of becoming adjusted to changing surroundings, it is the product of the interaction of all the elements of its environment. A change of any one of such elements requires a readjustment of the entire system unless such a change is at once offset by another which in its effects is antagonistic to it. If this is true, the necessity of possessing some facts or knowledge concerning the composition and the transformation of compounds in the plant in connection with those absorbed from the media surrounding it, is absolutely imperative. Anyone who has

attempted such analyses can realize the difficulties to be encountered without being told about them. It is not sufficient to make determinations on whole plants *en masse*; the several parts must be considered separately in as minute detail as possible, and then all must be related to the whole. Particularly is this true in relation to leaves and stems, when investigating the carbohydrate situation in a series of tests. Brief reflection will render obvious the fallacies of judgment which are likely to arise, especially when samples are collected during the day following a period of sunshine. The speed of digestion of the more complex carbohydrates (if any have been synthesized) and of their translocation is widely variable depending upon the other nutrients present. The presence of equal quantities of polysaccharides, indicated by analyses of material taken at any particular moment, in itself could by no means be interpreted as indicating an equivalent rate of synthesis, utilization, or storage of such products. These latter points could be determined only by a long series of analyses under varying conditions, or through indirect methods quantitatively measuring respiration, carbon fixation, and the like. Caution must be observed, also, in attempting interpretations of the analyses of plants already in any particular state or condition, the cause of which it might be desired to determine; it is only through the knowledge of a *series* of effects that causes can be deduced. For example, an analysis of fruit buds on any kind of fruit tree made during the winter or early spring will not furnish sufficient evidence on which to formulate a theory as to the nutrient relations necessary for their differentiation or presence. Instead, a number of observations from spring to winter are essential, for it is more than probable that the conditions determining meristematic differentiation are quite different from those accompanying the further development of the parts in question after initial differentiation, and the conditions for flowering may not be those for fruit setting and development. In fact, if our proposals are of any value or are true, the conditions for the production of the various results can not be the same.

But it is unnecessary to dwell on the complications of the problem to the extent that it may seem too large even for the beginning of an attack. The question may be asked, how is any knowledge of the relationships of vegetation and reproduction significant to practice? In reply it may be stated that it is at the very foundation of the whole matter of plant production, for on it rests the real understanding of such problems as cultivation, fertilization, irrigation, propagation, pruning (regeneration), phases of disease control, and many others. It has been dangerously easy to suggest interpretations of many of the results from these various practices upon a hypothetical basis; but, lacking still an abundance of carefully worked out experimental evidence, little is to be gained from a mere theoretical consideration of the probable or possible points involved beyond establishing working bases. Certain points of attack become obvious at once to anyone

really giving the problem thought. Even the working horticulturist, whether he be florist, vegetable gardener, or fruit grower, is constantly contributing excellent experimental evidence, and is more than eager for some rational means by which he can interpret it, at least to the point of knowing how to eliminate unprofitable practices on some fundamental basis. It is our duty and privilege to learn the effects of various practices, then to eliminate those which are mutually antagonistic to the gaining of any desired end and to utilize only those which are mutually supplementary. What could be more desirable from the economic standpoint, or, in other words, more practicable?

In conclusion, then, it seems that the most needed essential to further extension of knowledge on the effects of varying metabolic conditions on the modification of vegetative and reproductive functions is the coordination of our knowledge of external and internal conditions by those having the means, technique, and willingness to do this work. The working out and making available for study of the range effects of many more elements and compounds than the very few which are known at present is particularly desirable, so that it may be possible in the future to deal with tangible materials rather than with hypothetical proposals.

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